

A LATE CRETACEOUS SHARK COPROLITE WITH BABY FRESHWATER TURTLE VERTEBRAE INCLUSIONS

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ABSTRACT: A small (3.4 cm) coprolite from the Upper Cretaceous (middle Campanian age) Coachman Formation in South Carolina, contains six cervical vertebrae from a very small, freshwater, trionychid turtle. Four of the vertebrae included in the coprolite are aligned and partly articulated. The coprolite shows typical selachian heteropolar shape with traces of spiral morphology, and is attributed to one of several common lamniform shark taxa in the associated marine fauna, most probably *Squalicorax kaupi*. Based on the minute size of the included vertebrae, with the largest 4.5 mm long, the turtle must have been very small and likely newly hatched. Assuming the selachian producing the specimen was a marine or estuarine species, this coprolite specimen indicates that the shark was feeding in or proximal to a fluvial environment, as observed in modern species of *Carcharhinus*. Given the small size of the coprolite, the shark was likely also small, suggesting that a juvenile Late Cretaceous shark was feeding far upstream, perhaps near its pupping area.

INTRODUCTION

The history of studies of coprolites is long and extensive, tracing back to the early nineteenth century (e.g., Buckland 1829, 1835; DeKay 1830; and see Duffin 2012 for an historical summary). Indeed, William Buckland (1829) coined the term “coprolite.” The study of coprolites has gained renewed interest in modern studies due in large part to the inherent paleoecological information regarding feeding and predation present in ancient feces (e.g., Hunt et al. 1994; Chin et al. 2003; Friedman 2012; Milàn et al. 2012). Vertebrate coprolites recovered from terrestrial bone beds have received more attention, probably because of the common interest in larger carnivores (Chin 2002), especially dinosaurs (Thulborn 1991; Chin et al. 1998) and crocodylians (Sawyer 1981; Milàn 2010; Lucas et al. 2012). Nevertheless, marine vertebrate coprolites are very common in a wide range of siliclastic and chalk deposits. Among these, the characteristically spiral or scroll-shaped coprolites of selachians are among the most easily recognized and have been intensely studied (e.g., Buckland 1836; McAlister 1985; Coy 1995; Stringer and King 2012).

The specimen in the present study, ChM PV8998, is deposited in The Charleston Museum, South Carolina. It is identified as a very small selachian coprolite, based on its overall morphology, occurrence in a marine deposit, and apparent phosphatic composition (discussed below). As with many selachian coprolites (Diedrich and Felker 2012), it contains bone inclusions. However, as a novel occurrence, the identifiable bone inclusions in ChM PV8998 consist of six aligned vertebrae, four of which are well enough preserved to be identified as cervicals (i.e., neck vertebrae) from a very small, hatchling-sized, trionychid turtle, a freshwater (occasionally brackish) clade. The four well-preserved vertebrae are aligned on one side of the specimen and may partly be in original articulation. The six total vertebrae are evidently from a single individual and can be identified to their anatomical positions, allowing extrapolations of the length of the prey's neck, and thus the animal's original size. Specimen ChM PV8998 is important in offering new behavioral insights into Late Cretaceous sharks.

GEOLOGICAL SETTING

The coprolite specimen ChM PV8998 was collected in 2004, in Darlington County, South Carolina (Fig. 1, Site 1), from a lag deposit in a small sand quarry operated by the Stokes Sand and Gravel Company until early 2006 (herein referred to as Stokes Quarry). The lag deposit was derived from the middle Campanian Coachman Formation (Gohn 1992; Christopher and Prowell 2010). At the quarry site, the Coachman Formation was entirely subsurface, but core samples taken at the quarry floor show mixed detrital sediments, predominately dark claystone beds interbedded with well-sorted, glauconitic, fine quartz sandstone in flaser beds ranging from a few millimeters to 2.0 cm in thickness (Schwimmer et al. 2015). The productive area for vertebrate fossils was a small site adjacent to the east end of the quarry. Fossils were found by surface collecting among piles of lag deposit material excavated during commercial quarrying operations, along the north bank of a large pit flooded subsequent to earlier excavations at the quarry.

The age of the lag and associated Upper Cretaceous material at Stokes Quarry was determined from an auger hole on the floor of the quarry approximately 3.0 m below the original ground surface and 1.5 m above the water level of the pit. The drill log recorded 4.3 m of Pliocene sediments (determined as discussed below) overlying 4.9 m of Upper Cretaceous sediments. The age of the Upper Cretaceous deposits was determined from pollen extracted from auger samples and referred to the regional Hf (*Holkopollenites forix*) Pollen Zone (Fig. 2) of Christopher and Prowell (2010). This pollen zone occupies the middle Campanian, which conforms well to the age of associated marine vertebrates in the quarry assemblage, notably the presence of the giant crocodylian *Deinosuchus rugosus* (Schwimmer 2002). The Upper Cretaceous sediments in the quarry are overlain by Pliocene marine deposits containing a rich assemblage of marine mollusk shells, foraminifera, and ostracods, which indicate a pre-Duplin (late early to early middle Pliocene) age for this overlying unit (Schwimmer et al. 2015).

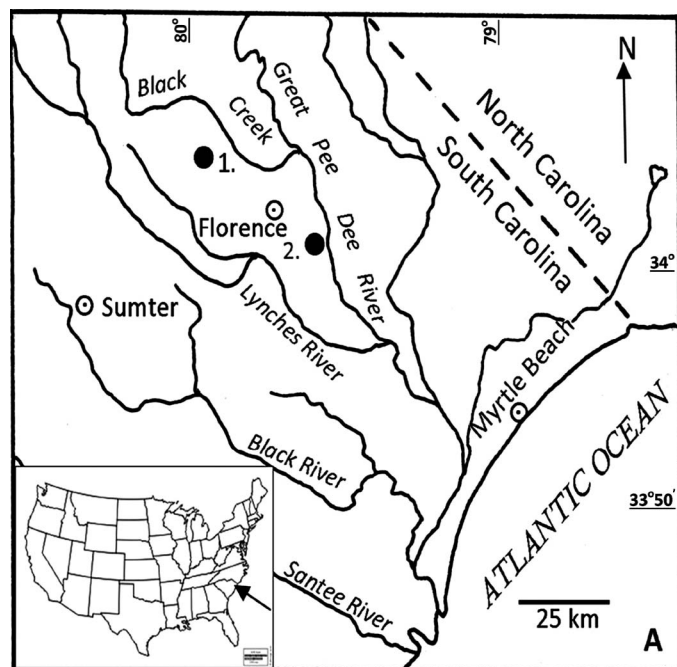


Fig. 1.—Locality map of northern coastal South Carolina, showing locations of Stokes Quarry (1) in Darlington County and Burches Ferry (2) in Florence County.

Stokes Quarry has yielded numerous Late Cretaceous marine and non-marine tetrapod fossils (Schwimmer et al. 2015). The quarry has also yielded abundant marine fish teeth, including those from sharks and bony fishes. The presence of marine turtles, mosasaurs, plesiosaurs, sharks, and marine bony fishes in the fauna indicates that the sediment was deposited in a pericontinental marine setting, whereas the presence of a non-marine tetrapod component (freshwater turtles, non-avian dinosaurs, crocodylians) indicates proximity to freshwater and terrestrial sources. The collective vertebrate assemblage indicates this was likely deposited in an estuary or other fluviially influenced nearshore marine setting (Schwimmer et al. 2015). Another site sampling the Coachman Formation in the same county in South Carolina (Cicimurri 2011) yielded a similar mix of terrestrial and shallow-marine vertebrates.

The fishes from Stokes Quarry have not been formally described, but teeth from the cosmopolitan lamniform species *Squalicorax kaupi* were among the most common fossils in the quarry. It is also noteworthy that Cicimurri (2007) reported two species of *Squalicorax* to be very common at Burches Ferry (Fig. 1, Site 2) on the Pee Dee River, in the superjacent (upper Campanian) Donoho Creek Formation of South Carolina (Fig. 2).

MATERIALS AND METHODS

The Coprolite

Coprolite ChM PV8998 is small, with antero-posterior length of 3.4 cm and the widest dimension 2.4 cm. Although the specimen is ablated on some surfaces, it appears to be overall intact with regard to the length and maximum width. It was judged too small to sample destructively for mineral composition without possibly destroying the unique inclusions; however, the very dark coloration of the coprolite (Fig. 3A) and its association in a phosphatic, glauconitic marine sand deposit with numerous similarly colored fossil bones and other coprolites, presumes that the composition is apatitic, as is typical of carnivorous vertebrate coprolites (Chin 2002). The overall morphology of ChM PV8998 (Fig. 3)

is heteropolar (defined below), with the tapered end presumed to be posterior (i.e., toward the anal direction; Hunt and Lucas 2012).

Coprolites from neoselachians (i.e., sharks, rays, and skates) are typically spindle-shaped, larger in diameter toward the anterior end, heteropolar (i.e., with one end, usually posterior, tightly coiled), or less often amphipolar (i.e., with relatively even coiling along the length; Hunt and Lucas 2012; Diedrich and Felker 2012). As with most marine and aquatically deposited coprolites, they do not show a flattened surface that would indicate deposition on a firm (i.e., terrestrial) surface. When originally deposited, prior to any diagenetic changes, selachian coprolites are calcium and phosphate-rich, reflecting a carnivorous diet (Chin 2002). Along with coprolites attributed to bony fishes, selachian coprolites often contain bone inclusions (Friedman 2012; Diedrich and Felker 2012), largely due to the lack of crushing dentition in most sharks. Most notably, selachian coprolites are characterized by their spiral or scroll morphologies imposed by the morphology of their intestines. The details of spiral versus scroll-shaped morphology among selachian coprolites has received a great amount of study (e.g., Williams 1972; McAlister 1985, Hunt and Lucas 2012; Stringer and King 2012). In Late Cretaceous marine fossil collections, spiral specimens are more commonly reported (e.g., Stewart 1978; Coy 1995; Eriksson et al. 2011) than scroll shapes. This fact may reflect a greater abundance of more basal galeomorphs (i.e., larger, typically nektonic sharks) at that time, especially the common Late Cretaceous Lamniformes such as *Scapanorhynchus*, *Cretalamna*, and *Squalicorax* (the latter tentatively assumed to be a lamniform; Shimada and Cicimurri 2005). Their modern relatives produce largely spiral feces (Stringer and King 2012).

The external surface of ChM PV8998 indicates a history of at least two sequences of ablation: a first event which split off part of one side near the posterior end, and secondary processes of rounding and general surface erosion. The four best-preserved vertebrae in this coprolite (Fig. 3A, B) occupy a shallow recess in the posterior region, suggesting that they were exposed following (and perhaps causing) the splitting event which removed part of the posterior surface. It is likely that the excellent preservation of these vertebrae is due to their occurrence in the recess, which shielded them from significant ablation after exposure. Two additional, much ablated, vertebrae are exposed on the opposite side near the posterior end (Fig. 3C), and these are located on a protuberant surface of the coprolite. Ablation of much of the external surface of the coprolite is interpreted to have effaced most evidence of the original spiral structure, although a vestige remains (best observed in Fig. 3C).

Vertebrae Inclusions

The vertebrae included in coprolite ChM PV8998 are elongate, with notably long anterior and posterior zygapophyses. The vertebral centra are long and narrow, opisthocelous (i.e., concave posteriorly), with very slight articular condyle projections and concavities at the opposite ends. ChM PV8998 contains six such bones, and an additional bone fragment at the extreme posterior tip of the coprolite, which may represent a remnant of the seventh vertebra. All of the preserved vertebrae are small, ranging from 3.0 to 4.5 mm centrum length (Table 1), with the ablated specimen at the posterior end approximately 1.5 mm long.

The four well-preserved vertebrae on one side of ChM PV8998 have the ventral surfaces facing outward (Fig. 3A, B), whereas the two additional vertebrae on the opposite side are too ablated to determine their surface orientations (Fig. 3C). The long axes of the four vertebrae on the side shown in Figure 3A and 3B are all oriented parallel to the long axis of the coprolite, and comprise the bulk of the tapered end. Two of these vertebrae are apparently in original articulation based on their relative size and position.

Overall, the vertebrae are remarkably well preserved and, based on the extreme elongation of the vertebral centra and the conformation of the

AGE (Ma.)	Series	Stage	Nannofossil Zone	Pollen Zone	SC Formation	Study Site		
70	UPPER CRETACEOUS (part)	MAASTRICHTIAN	CC26	<i>Sparganiaceapollenites uniformis</i> (Su)	SAWDUST LANDING			
			CC25	<i>Holkopollenites chemardensis</i> (Hc)	STEEL CREEK / PEEDEE			
				<i>Carolinapollis triangularis</i> (Ct)				
72		CAMPANIAN						
			CC23	<i>Osculapollis aequalis</i> (Oa)	DONOHO CREEK		BLACK CREEK GROUP (part)	Burches Ferry
CC22								
77			CC21	<i>Complexiopollis abditus</i> (Ca)	BLADEN			
			CC20	<i>Holkopollenites forix</i> (Hf)	COACHMAN			
80			CC19	<i>Holkopollenites propinquus</i> (Hp)	CANE ACRE			
			CC18		CADDIN			
83								

FIG. 2.—Chronostratigraphic sequence of Campanian and Maastrichtian (Upper Cretaceous) deposits in South Carolina. Age data (Ma = millions of years) from Ogg and Hinnov (2012); nannofossil zones from Sissingh (1977); South Carolina pollen zones and stratigraphic correlations from Christopher and Prowell (2002, 2010).

articulating surfaces, both shared derived characters of the family, it is apparent that these are cervical vertebrae from a trionychid turtle (Romer 1956; Meylan 1987). The Trionychidae are post-Jurassic (Meylan 1987), globally distributed, predominantly freshwater cryptodire turtles (Ernst and Barbour 1989). They are characterized by leathery skin covering the carapace, rather than the thin, hard scutes of other turtles—hence their common name, “soft-shelled turtles.” The carapace and plastron bones in trionychids are also distinguished by having deeply pebbled surface sculpture lacking evidence of scute sulci (Meylan 1987), making even small fragments of trionychid shell readily identifiable at least to the family level. They are generally freshwater inhabitants, but a few species are salt-water tolerant, habitually moving into and out of the shallow marine environment (Ernst and Barbour 1989; Ip et al. 2012). This explains why their larger bones are often found in nearshore marine deposits. There is no evidence, however, that hatchling or very young trionychids inhabit brackish or marine environments.

Nearly all post-Triassic turtles, including trionychids, have eight cervical vertebrae (Romer 1956). However, unlike other turtles, trionychid cervicals 2 (C2) through 7 (C7) are opisthocelous and extremely elongated. The eighth (C8) in trionychids is distinctive among turtle cervicals in having no central articulation with the anteriormost thoracic

vertebra (Meylan 1987), thus allowing extreme upward flexure of the entire neck. C8 is also notably shorter and broader than the other cervicals. Assignments of positions in the cervical series (Table 1) for the inclusions in ChM PV8998, are based on sizes, relative position in the coprolite, size and shape of the neural openings, and overall morphologies of the vertebrae.

RESULTS

As noted above, coprolites from a wide variety of neoselachians may contain incompletely digested bones and scales showing various degrees of dissolution. However, essentially undigested bones in putative selachian coprolites are rare. To our knowledge multiple bone inclusions in association have not previously been reported from a selachian coprolite.

The vertebrae present in ChM PV8998 are evidently a nearly complete set of trionychid cervicals (Fig. 4), comprising positions C2-C7. The small bone fragment at the extreme posterior end of the coprolite that appears to be in articulation with the vertebra interpreted as C2, may be the centrum of the atlas (C1). Based on their relative sizes and obvious proximity, they almost certainly come from a single individual; however,

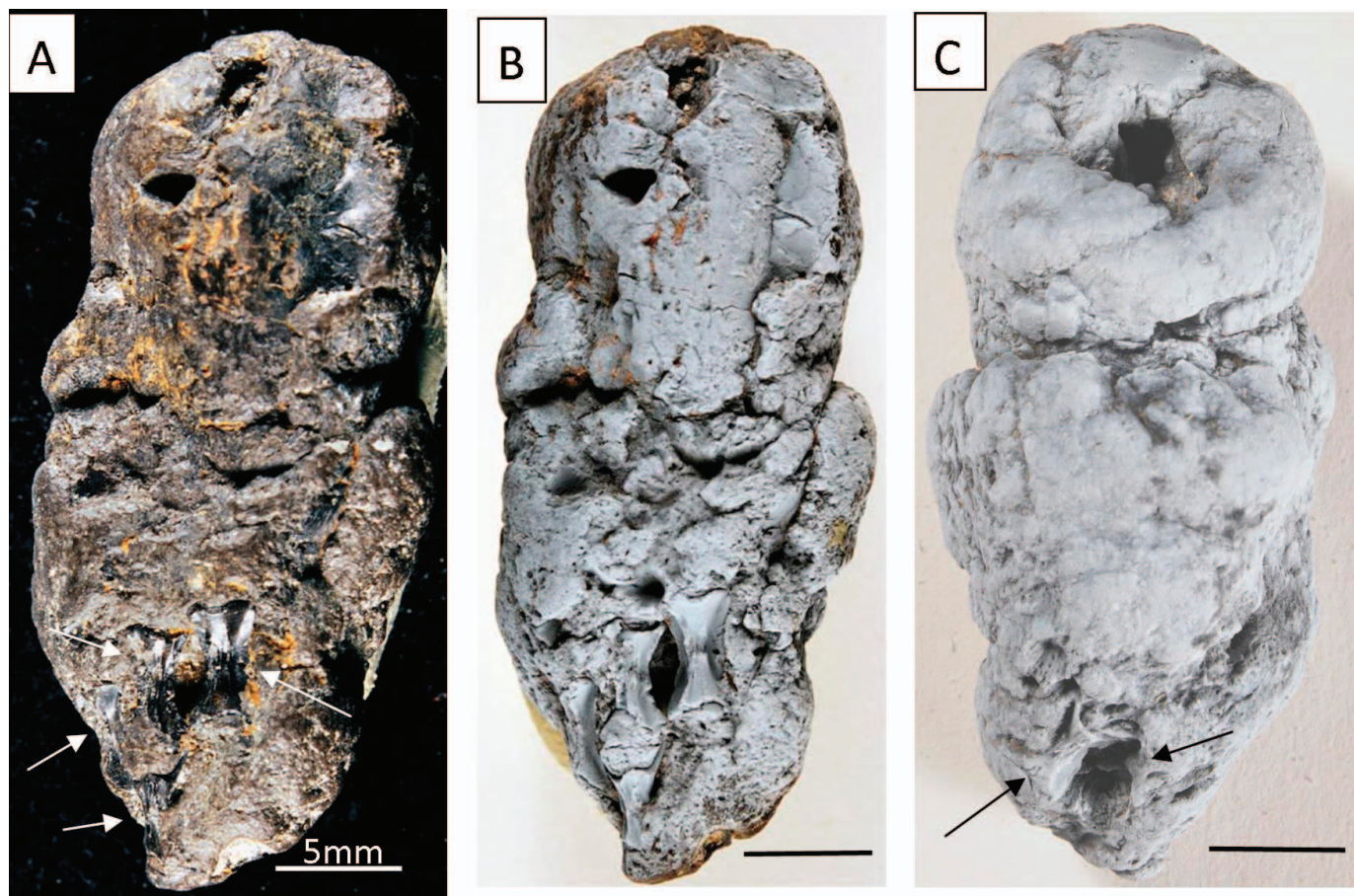


FIG. 3.—Overall views of coprolite ChM PV8998. **A)** View of one side showing four associated, well-preserved turtle vertebrae (arrows) at the bottom (posterior) end. **B)** View A whitened with ammonium chloride sublimate. **C)** Opposite side of ChM PV8998, whitened with ammonium chloride sublimate, showing vestige of spiral morphology and one additional vertebra (arrow), partly visible toward the posterior end.

identification below the family level of the specific trionychnid represented by the inclusions in ChM PV8998 is not possible for several reasons. First, the generic taxonomy of Cretaceous trionychnids is poorly constrained (Gardner et al. 1995; Brinkman 2003; Danilov and Vitek 2013), and is based largely on shell morphology. Second, even if the shell-based taxonomy were well delimited, Cretaceous trionychnid cervical vertebrae have not been systematically correlated with known genera, so it is

unclear if generic level identifications are possible from vertebrae alone. Third, to date, all of the trionychnid specimens identified in the Upper Cretaceous of eastern USA are indeterminate to genus because all reported fossils (Baird 1986; Schwimmer 1986; Hartstein et al. 1999; Schwimmer et al. 2015) are isolated carapace and plastron fragments. Generic assignments of trionychnid turtles depend heavily on character states of the plastron, undeterminable in the eastern specimens (Schwimmer et al. 2015).

By convention (*vide*, Baird 1986), pebble-textured turtle shell fragments in Upper Cretaceous deposits in eastern USA have been assigned to species of the form-genus “*Trionyx*” for lack of diagnostic material: the name was inherited from older literature (e.g., Leidy 1851; Cope 1869). Gardner et al. (1995) synonymized many prior generic assignments of “*Trionyx*” and *Aspideretes* (another traditional form-generic assignment) into *Aspideretoides*, based on the hypothesis that the presence or absence of a preneural bridge on the plastron is taxonomically significant, rather than a variable character. *Aspideretoides* is currently a generic identification in wide use for non-diagnostic Late Cretaceous specimens in areas including western North America (Gardner et al. 1995) and Eurasia (Danilov and Vitek 2013), as well as for Paleogene specimens in southeastern USA (Holroyd et al. 2005).

Although knowledge of the generic and specific identification of the cervicals in ChM PV8998 would obviously be of use in estimating the potential adult body size of the trionychnid consumed by the shark, absent

TABLE 1.—Measured lengths of cervical vertebrae included in coprolite ChM PV8998. Lengths are measurements of vertebral centra visible in ventral view, rounded to the nearest 0.1 mm. C6 and C7 are poorly preserved and measurements reported are as reconstructed.

Trionychnid Cervical Vertebrae Included in ChM PV8998	
C1? (fragment)	1.3 mm
C2	3.0 mm
C3	3.2 mm
C4	3.8 mm
C5	4.0 mm
C6	4.5 (reconstructed)
C7	4.5 (reconstructed)
Total Cervical Length:	~27.5 mm

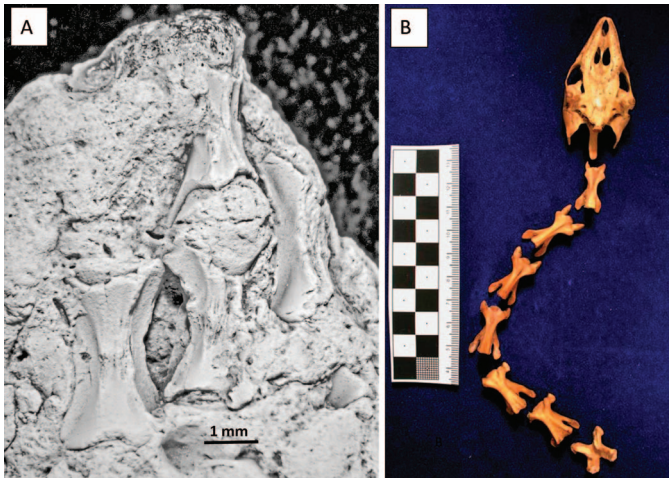


Fig. 4.—A) Close-up view of associated turtle cervical vertebrae in coprolite ChM PV8998, image reversed for comparison with Figure 4B (thus the posterior end of the coprolite here is up). These vertebrae are tentatively identified as C2 to C5. B) Ventral view of cervical vertebrae C2-C8 and skull of extant trionychid *Apalone spinifera*, for comparison with vertebrae in Figure 4A (unit of smallest scales in millimeters).

that it is still possible to make reasonable assumptions about its state of maturity. Modern adult trionychid turtles may be quite large, with mature straight carapace lengths (SCL: i.e., bridging the dorsal curvature) ranging from approximately 18 cm up to 95 cm in the largest species *Trionyx triunguis*, approaching the size of sea turtles (Ernst and Barbour 1989). Among more common, larger Upper Cretaceous trionychid species with known carapace dimensions, *Aspideretoides splendidus* in the Campanian Judith River Formation of Alberta is reported to have shell widths reaching 69 cm (Gardner et al. 1995; although SCL was not specified, the carapace outline is subquadrate, indicating a nearly equal shell length). The relative sizes of common trionychid specimens found in eastern Upper Cretaceous deposits indicates that typical individuals had sizes corresponding with larger *Aspideretoides* species from better-documented regions of western North America and Eurasia.

The reconstructed articulated length of the six vertebrae (C2-C7) in ChM PV8998 is approximately 23 mm in length (Table 1). The two vertebrae missing from the neck can be estimated to add 4.5 mm to the total length of the neck, because in living trionychids, such as *Apalone spinifera* (Fig. 4B), C1 is typically short and C8 approximates the length of mid-cervical vertebrae (Shiel 2003). The overall length of the neck thus approximates 27.5 mm, which also provides a rough estimate for the carapace length, which is approximately the same length as the extended neck in trionychids. Thus, the overall size of the turtle preserved in ChM PV8998, adding head and tail, in typical posture, would be approximately 60 mm long, with SCL of ~ 27.5 mm. It is evident, therefore, that the vertebrae come from an extremely small trionychid, regardless of the species.

Among living trionychid species, hatchling sizes are relatively uniform, in contrast to the much more variable sizes of mature individuals. The widespread *Apalone spinifera*, among the larger North American recent species, ranges up to 45 cm SCL, with hatchlings ranging from 30–40 mm (Ernst and Barbour 1972). Oddly, the largest extant trionychid, *T. triunguis*, is reported to have hatchlings with SCL averaging 30 mm (Ernst and Barbour 1989). Thus, adult size is poorly correlated with hatchling size. Therefore, regardless of the adult size of the Cretaceous trionychid in study here, we can assume that with an estimated CPL equal to the cervical length (i.e., 27.5 mm), the individual whose cervicals are included in ChM PV8998 hatched shortly before death.

DISCUSSION

Origin of the Coprolite

Many living neoselachians are euryhaline (i.e., tolerant of a wide range of salinities), including primarily fresh- and brackish-water species (Martin 2005). However, the majority of selachians in low-salinity habitats are batoids and juveniles of larger species (Martin 2005; Dowd et al. 2010). Fewer Galeomorphii (i.e., typical predatory sharks, *sensu* Compagno 1973) are tolerant of low salinity environments. Noteworthy examples of these euryhaline species include the widespread and common bull shark (*Carcharhinus leucas*; Ortega et al. 2009; Reilly et al. 2011) and the closely related sandbar shark (*C. plumbeus*; Merson and Pratt 2001). Bull sharks are exceptional among larger predaceous sharks in their ability to live in full marine to entirely freshwater river and lake environments, occasionally ranging more than 1000 km upstream from the ocean (Thomerson 1977). The ability of a shark to migrate from high to low salinities (Ortega et al. 2009), or to live in freshwater, requires a considerable number of metabolic modifications relative to typical galeomorphs, notably the ability to osmoregulate the respiratory tissues (Reilly et al. 2011), body fluids and internal organs (Pillans et al. 2005).

There is no specific proof that any Late Cretaceous galeomorph selachians were tolerant of low-salinity environments. However, the abundance of teeth from several lamnoid taxa in eastern Coastal Plain sites interpreted to have been estuarine and back barrier lagoon settings (Gallagher et al. 1986; Case and Schwimmer 1988; Schwimmer 2002), suggests that these were likely from euryhaline sharks. Among more than three dozen reported galeomorph neoselachian species in the Campanian deposits of eastern USA (Cappetta and Case 1975; Case and Schwimmer 1988; Robb 1989; Cicimurri 2007), the overwhelming majority of identifiable material (largely teeth) comes from two lamnoid genera: *Scapanorhynchus* and *Squalicorax*. Between these two shark genera, *Squalicorax* species (*S. kaupi*, *S. yangaensis* or *S. pristodontus*) are the best candidates for the source of ChM PV8998 because they all have cutting-type dentition (Cappetta 1987). They possess serrate, robust, recumbent teeth, similar to those of living tiger sharks (*Galeocerdo cuvier*), interpreted to be adapted for generalist predation including harder-boned prey such as turtles (Schwimmer et al. 1997; Becker and Chamberlain 2012). The other common selachians in the Campanian of the eastern Coastal Plain, *Scapanorhynchus* spp., had slender, elongate, tearing-type teeth (Cappetta 1987), much more suited to piscivory. Also, as noted previously, *Squalicorax kaupi* teeth were very abundant at Stoke's Quarry (Schwimmer et al. 2015), as well as at a nearby Campanian site (Fig. 1) at Burches Ferry, South Carolina whereas *Scapanorhynchus* teeth are oddly absent (Cicimurri 2007).

Squalicorax kaupi was a mid-to-large size galeomorph selachian species, with average adult lengths estimated at 3.0 to 3.5 m (Schwimmer et al. 1997; Shimada and Cicimurri 2005), extrapolated from partial and nearly complete skeletons. It is not explicitly possible to correlate coprolite size and body size in a fossil selachian, but it is assumed here that a 3.4 cm coprolite would come from a small, young individual in a shark species that reaches 3.0 m or greater in length.

Paleoecology of the Coprolite

Based on assumptions for the origin of ChM PV8998, especially the sizes of both the shark producing the coprolite and the consumed trionychid, we hypothesize that a small galeomorph shark, likely a recently born lamniform, was feeding proximal to a freshwater or terrestrial site where trionychid turtles were hatching. This scenario assumes that the collecting site on the Late Cretaceous South Carolina coast was most likely an estuary or fluvially influenced embayment (Schwimmer et al. 2015).

Squalicorax species have been identified as frequent scavengers (Schwimmer et al. 1997). Although there is no information inherent in ChM PV8998 to specify whether the feeding was predatory or scavenging, the very well-preserved condition of the vertebrae, with the neck remaining in articulation, suggests that the baby turtle was not significantly decomposed before being eaten. Thus, a predatory feeding event is most probable.

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